

Studies in the Helminthocladiaceae, III

*Liagoropsis*¹

MAXWELL S. DOTY² and ISABELLA A. ABBOTT³

IN THE FIRST PAPER in this series of studies of the Helminthocladiaceae (Doty and Abbott, 1961), we have shown that, in two species of *Helminthocladia* from Hawaii, the female reproductive structures are generally similar to those described by other workers for other species in the genus, and that vegetative structures such as internal cortical rhizoids may be used to distinguish at least the Hawaiian species. In the second paper of this series (Abbott and Doty, 1960) a new genus, *Trichogloeopsis*, was described as containing three species, one new and two transfers from the genus *Liagora*. They share a major character in common, that of sterile rhizoidal extensions of the gonimoblast, but again the three species may be distinguished from each other by their vegetative structures.

Liagoropsis was first described⁴ by Yamada (1944) from material collected in Taiwan (Formosa). The type and only known species was *L. maxima*. The type specimens of all the

species concerned here have been studied by us and we have included illustrations⁴ of them (Figs. 1–4) when they have not been illustrated before. We have studied two thalli from Yamada's collections of the type species: the type (Yamada, 1944: fig. 5), a male thallus; and a cotype,⁵ a female specimen. It is upon the characteristics of the female thallus that the main description of the generic taxon rested. In examining specimens (Table 1) of eight of the nine collections which we believe constitute *Liagoropsis*, we are of the opinion that the structural vegetative differences seen, whether external or internal, are without taxonomic significance at either the generic or specific level. Thus, we believe that the genus can be amply delineated on the basis of characters possessed by the female reproductive apparatus alone, and that *Liagoropsis* as known at present should be considered monotypic.

¹ This work was made possible through financial assistance from the National Science Foundation on Contract #G3833, from the Philippine National Research Council by funds for expenses provided under Republic Act 1606, and from the Graduate Committee of the University of Hawaii.

For the loans of critical materials used in this study we wish to thank Y. Yamada, Hokkaido University; P. Bourrelly, Museum National d'Histoire Naturelle, Paris; T. Norlin, Lund University; The Botanical Museum of the University of Copenhagen; T. V. Desikachary, R. Subramanyan, and V. Krishnamurthy, Madras University; Laura Huerta, Escuela Nacional de Ciencias Biológicas, Mexico City; and L. Williams, Duke University. We are also indebted to Gregorio Velasquez, University of the Philippines, who accompanied the senior author and made possible some of the field trips in the Philippines.

² Department of Botany, University of Hawaii, Honolulu, Hawaii.

³ Hopkins Marine Station of Stanford University, Pacific Grove, California.

⁴ Desikachary published (1957: fig. 1) a photograph of his material. Yamada (1944: fig. 5) has an excellent drawing of the type of *Liagoropsis maxima*, which specimen we have studied. Boergesen published (1909: plates I and II, respectively) photographs of one of his sheets of *Nemalion schrammi* and of the type of *Nemalion longicolle*.

⁵ By using "cotype" here the authors mean not to derogate the more precise terms *isotype* and *paratype*. The thalli under consideration are parts of the same collection but were separate thalli and of different sex. To use isotype would be akin to using this term for both the male and female branches collected at one time from, respectively, separate staminate and pistillate flower-bearing trees. To use paratype would imply that in the original place of publication this was a specimen other than the holotype cited with the original description. This specimen was not cited by Yamada although the dioecious nature of the species as represented by the specimens examined was mentioned and aspects of both the male and female thalli were described.

In external appearances (Figs. 1-4) *Liagoropsis* resembles some species of *Liagora* (Abbott, 1945), especially *L. farinosa*, but it is more robust and taller, and the branches are more irregular than those of any species of *Liagora* known to us. In its slightly calcareous nature it lies between the noncalcareous genera, such as *Nemalion* (which may have carbonate deposits in the base of the thallus), and generally strongly calcified genera, such as *Trichogloea* and *Liagora*. The fresh thalli resemble *Trichogloea requienii* and *T. lubrica* or the *Trichogloeopsis* species in texture, being soft and mucilaginous to gelatinous, though limy or slightly calcified. The dried thalli do not reveal this very soft nature but in herbarium specimens that have been dried without decalcification the liminess shows, usually in a reticulate pattern.

Yamada distinguished the genus from *Liagora* on the basis of the slight amount of calci-

fication possessed by *Liagoropsis*, the paucity of involucre filaments, and the equality of the sometimes terminal carpogonial branches to vegetative branches. From his illustrations of the reproductive features it is clear at once that his genus is indeed different from *Liagora*. The extent of these differences was not known, however, in reference to the other criteria used for distinguishing genera among the simpler Nemalionales, and our present study was made largely to gather further information in this regard.

Table 1 reveals the geographic distribution of this genus. In consideration of these locations it appears that one can expect to find this genus most often in the same areas where one finds the greatest degree of coral development, that is, in the warmer parts of the western Pacific and the western Atlantic. Yet it is not reported by Taylor (1942), Bernatowicz (1952 a,b),

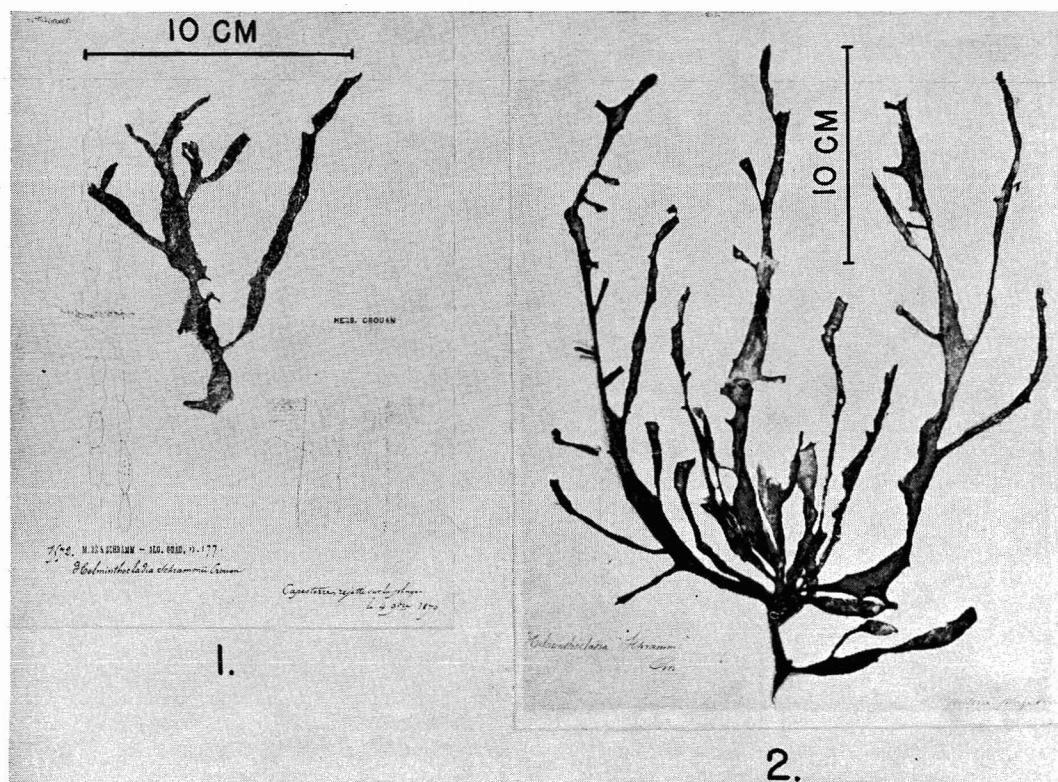
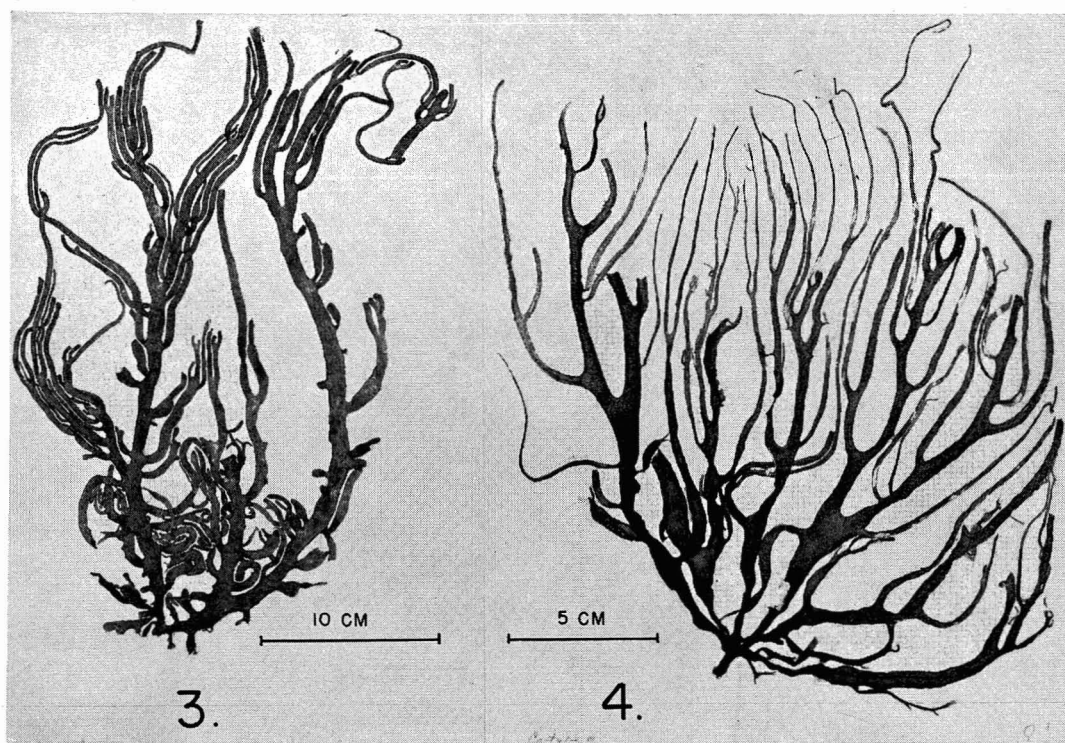


FIG. 1, 2. Photographs of female carpogonial thalli believed to be representative and accepted as representative of *Liagoropsis Schrammi*; these are, respectively, the type and an isotype of *Helminthocladia schrammi*. Fig. 1, The type specimen in the Thuret herbarium. Fig. 2, The isotype bearing the number 21962 in the Agardh herbarium.



FIGS. 3, 4. Photographs of female carpogonial thalli believed to be representative of *Liagoropsis schrammi*. Fig. 3, M. Doty no. 16954 from the Philippines. Fig. 4, A cotype of *Liagoropsis maxima* from Y. Yamada's herbarium.

Collins and Hervey (1917), or Howe (1918, 1920) in their several floristic treatises of the western warmer Atlantic. Strangely enough it is not yet known, seemingly, from south of the equator except for the Williams collection. This is certainly due in part to a lack of habitats in the western Atlantic and Indian oceans south of the equator, but perhaps even more likely due to our lack of floristic information on these areas. However, it appears neither elsewhere in the studies of Boergesen nor in those of Weber Van Bosse, whose works on Indian Ocean and Indonesian algae were both intensive and extensive. The relative abundance of records from the Indian Ocean north of the equator is less easy to explain, unless it is the result of a greater collecting intensity in these waters.

DESCRIPTION AND DISCUSSION OF THE SPECIES

It is our intention to continue use of the oldest legitimate specific epithet published which

applies to the one species we feel should be recognized; and this is accepted here as "*schrammi*," validly published in the combination *Helminthocladia schrammi*, with the very poor description, "*Pourpre jaunâtre à l'état frais*," by Maze and Schramm (1870-77:177-178). As Boergesen (1909:4) points out, J. Agardh (1890:41), in treating this alga as a *Helminthocladia*, suggested it might better be treated as a member of the Chordariaceae (Phaeophyta). There seems to be no question, applying contemporary criteria, but that this is a member of the rhodophytan order Nemalionales, the classification, nomenclature, and nature of which are discussed below.

Liagoropsis schrammi (Maze et Schramm)
comb. nov.

Figs. 1-19.

BASIONYM: *Helminthocladia schrammi* Maze et Schramm. 1870-77. *Algues de la Guadeloupe*, 2^e ed., p. 177.

TYPE:⁶ Maze and Schramm (loc. cit.) say their only collection was found cast onto the beach at "Capesterre." It is accepted that the type of *Helminthocladia schrammi* was washed onto the beach at Capesterre, Guadeloupe (16° N, 62° 40' W), in November, 1870, collected, and later numbered "1572." The collection was said by Maze and Schramm to be of only one specimen. Possibly, this specimen was divided (Boergesen, 1909) into at least three parts, one deposited in the Thuret herbarium, a second in the general cryptogamic herbarium of the Museum d'Histoire Naturelle (Paris), and a third

in the Agardh herbarium. We accept the specimen (Fig. 1) in the Thuret-Bornet herbarium at the Paris Museum as the holotype. An isotype (Fig. 2) has been located, as number 31962, in the Agardh herbarium, but no third part has been located.

Nemalion schrammi (Maze et Schramm) Boergesen. 1909. Some new or little-known West Indian Florideae, I. Botanisk Tidsk. 30:4, pl. 1, text fig. 3 (obligate synonym, typonym).

Nemalion longicolle Boergesen. 1909. Some new or little-known West Indian Florideae, K. Botanisk Tidsk. 30:8, pl. 2, text fig. 4 (facultative synonym).

Liagoropsis maxima Yamada. 1944:19 ff., figs. 5, 6 (facultative synonym and generic holotype⁶). Cotype illustrated here as Figure 4.

Thalli up to 1 m tall, primarily pinnate (Fig. 3) to irregularly branched, becoming pseudo-dichotomously branched distally (Fig. 4); lightly calcified, soft and gelatinous; of multiaxial construction; central axes cylindrical, becoming compressed often up to 1 cm, or even 3.3 cm

⁶The type for the species, *Liagoropsis schrammi* (Maze et Schramm) Doty & Abbott, is a specimen (Fig. 1) deposited in the Paris Museum. We have had the privilege, through the courtesy of Dr. Pierre Bourrelly, of studying a fragment of this material, and Dr. Bourrelly provided us with the photograph for the figure given here. The type for the genus is the species *Liagoropsis maxima* Yamada, and through the courtesy of Dr. Yukio Yamada we have had the privilege of studying the male type specimen and a female cotype specimen (Fig. 4) from his herbarium.

TABLE 1

SOURCES OF INFORMATION, THE RELATED COLLECTION NUMBERS, AND
GEOGRAPHIC ORIGINS OF THE COLLECTIONS*

AUTHOR, CITATION, COLLECTION NUMBERS, AND IDENTIFICATION	POSITIONS OF KNOWN COLLECTIONS	
	Latitude	Longitude
1. <i>Nemalion schrammi</i> (Williams and Blomquist, 1947)	07° 35' S	34° 55' W
2. <i>Helminthocladia schrammi</i> (Maze and Schramm, 1870-77)	16° N	62° 40' W
3. <i>Nemalion schrammi</i> (Boergesen, 1909 [#1614])	17° 40' N	64° 50' W
4. <i>Nemalion longicolle</i> (Boergesen, 1909 [#1614])	17° 40' N	64° 50' W
5. <i>Liagoropsis schrammi</i> ([M. Doty coll. #16954])	13° 14' N	123° 46' E
6. <i>Liagoropsis maxima</i> (Yamada, 1944)	24° N	121° E
7. <i>Liagoropsis maxima</i> † (Desikachary, 1957)	12° N	93° E
8. <i>Liagoropsis schrammi</i> (Subramanyan [M. Doty coll. #19686])	11° 40' N	92° 40' E
9. <i>Liagoropsis schrammi</i> (Desikachary [M. Doty coll. #19687])	08° 48' N	78° 10' E

* The material reported (Huerta, 1960) as *Nemalion schrammi* seems to be, according to a communication from the author of that article and the material of the collection seen by the present authors, *Helminthocladia calvadosii* (Lamx.) Setchell.

† Specimens not seen.

broad. Assimilatory filaments thin, the cells cylindrical to obovate, frequently tipped with a hair, and then resembling those of *Liagora* rather than *Nemalion*. Terminal cells of vegetative filaments not specially differentiated. Male gametes becoming spherical, produced (Fig. 5) in grapelike superficial clusters. Male and female structures produced on the same or on different thalli. Carpogonial branch apparently a modified vegetative branch, or an outgrowth from the basal first or second cell of a vegetative system, or one member of a pair of branches arising (Figs. 6, 7) from the basal or second dichotomy in a vegetative branch, or in still other (but much more rare) cases a lateral branch of a vegetative system. In the order of these positions as given, the cell number in the carpogonial branch seems to decrease variably from eight to five cells. Carpogonial branches shorter than the vegetative branches near them and usually straight as in *Nemalion* rather than curved as usual in *Liagora*. Carpogonial branches usually with two (one to three) cells at the base (Fig. 6) similar to the other vegetative cells near them. Hypogynous cells three to five, forming a stalk below the carpogonium.

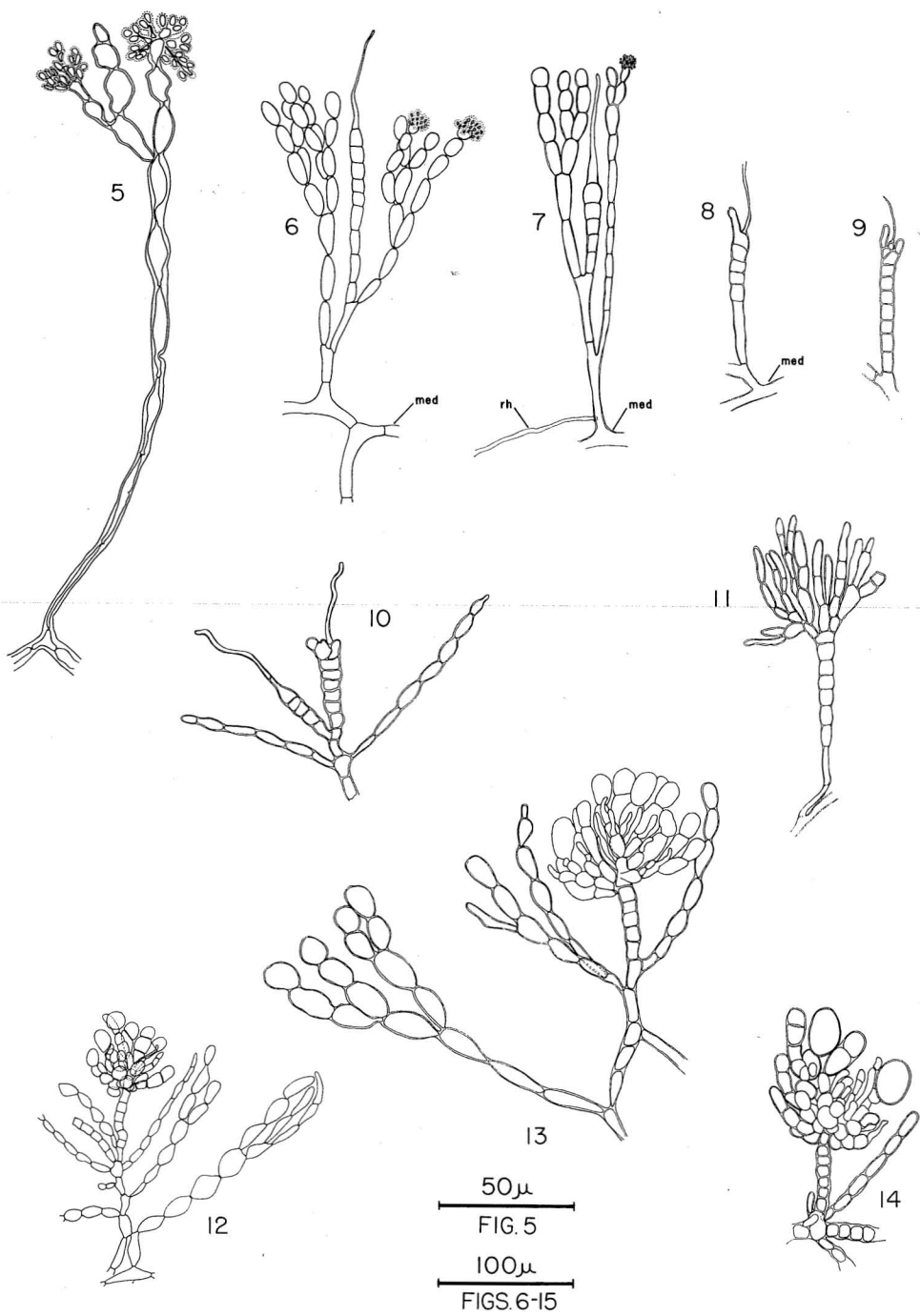
After fertilization the trichogyne separates from the zygote and withers away except at the base. The zygote itself does not always conspicuously divide transversely but produces prominent filaments (Figs. 8–10) rarely protruding horizontally from the carpogonial axes, usually protruding toward the thallus surface and often even nearly parallel to the trichogyne. Our observations are in general agreement with those of Desikachary (1957) who illustrates this process well. In some cases it seemed that the more basal carpogonial protoplasm had become highly vacuolated, pushing the gonimoblast-forming cytoplasm out into the developing gonimoblast filament initials without a previous division of the zygote. In other cases the zygote cytoplasm seemed to have become divided after much of the cytoplasm had collected in the apex of the carpogonium under the separated trichogyne but before gonimoblast filaments appeared. Clearly in the latter case a sterile stalk cell is produced between the hypogynous cells and the gonimoblast initial. Soon (developmentally) several more gonimoblast filaments are produced parallel to those first formed.

The upper part of the carpogonial cytoplasm was the only part seen giving rise to gonimoblast filaments, whether or not the cell had divided into two cytoplasts following fertilization. Very rarely, however, in older stages it appeared that some gonimoblast filaments had their origin below the line above which one would say the dense cytoplasm would have aggregated and separated by cell division after fertilization typically, but, in the poorly fixed material at hand, observations of a cytological nature could only lead to tentative conclusions.

The gonimoblast filaments at maturity are pseudo-dichotomously divided, perhaps up to as many as four times. The individual segments are rather straight and uniformly diverging throughout, yet always directed toward the surface of the thallus (Figs. 11–14) so that the mature gonimoblast forms an inwardly pointing cone of rather closely placed, rather straight and free filaments. The terminal carposporangia bear but one spore each. In age the carpospores may be gone from the terminal cells of the first-formed erect filaments. The empty carposporangia then form an apically colorless central mass surrounded by younger, secondary gonimoblast.

Desikachary (1957: figs. 1, 2, 4, 5) shows sterile or vegetative filaments arising from the base of some carpogonial branches. Neither he (1962) nor we consider these to be sterile filaments produced as special branches in association with the reproduction process, but rather as less well-developed vegetative branches. In the various materials examined we have found no sterile filaments developed around the gonimoblast from either the carpogonial branch or from the surrounding vegetative cells as is the case in *Trichogloea* or *Liagora*. However, from the base of the carpogonial branch there develop rhizoids which run in straight courses away from the supporting cells. From some mature gonimoblasts such rhizoids were seen protruding from the basal few cells in the carpogonial branch itself. We saw no such rhizoids arising from the carposporophyte.

The thalli collected by the senior author (Fig. 3) were attached to stones and sunken logs in 2–3 m of water off the mouth of a small stream near the village of Libog, Albay Province, Philippines (13° 14' N; 123° 46' 8" E), V-19-1958. Hundreds of thalli could have been col-



lected over a 0.25 hectare area. About 1 liter of specimens was preserved with strong formalin on the spot. It may be added, in passing, that Boergesen's (1909) materials came from a similar habitat.

The Philippine material on which the descriptive paragraphs above were written consists of herbarium sheets of the collection bearing the senior author's number 16954. The specimen deposited in the Bishop Museum herbarium in Honolulu, Hawaii, is presented here as Figure 3. Portions of the same collection, but not parts of the same thallus, are being distributed to the herbaria of the University of the Philippines, Hopkins Marine Station, Hokkaido University, Kagoshima University, Museum of Natural History (Paris), Copenhagen University, Lund University, University of California (Berkeley), Adelaide University, and Madras University.

OTHER SPECIMENS EXAMINED (Table 1): the type of *Helminthocladia schrammi* (Paris); specimens of Boergesen (Botanical Museum, Copenhagen) under the name of *Nemalion schrammi*; the type of *Nemalion longicolle* (Botanical Museum, Copenhagen); the type and cotype of *Liagoropsis maxima* (Y. Yamada's herbarium, Sapporo, Hokkaido); the specimen of Williams (Duke University, Durham, N. C.) from Brazil as *Nemalion schrammi*; specimens of Desikachary (University of Madras) from Tuticorin and of Krishnamurthy and Subramanian (University of Madras) from the Andaman Islands. There seem to be no specifically significant or consistent reproductive or vegetative differences between these materials.

Boergesen (1915) distinguished the more slender species, *N. longicolle*, on the basis of the solitary central or terminal position of the carpogonial branch from the broader species, *N.*

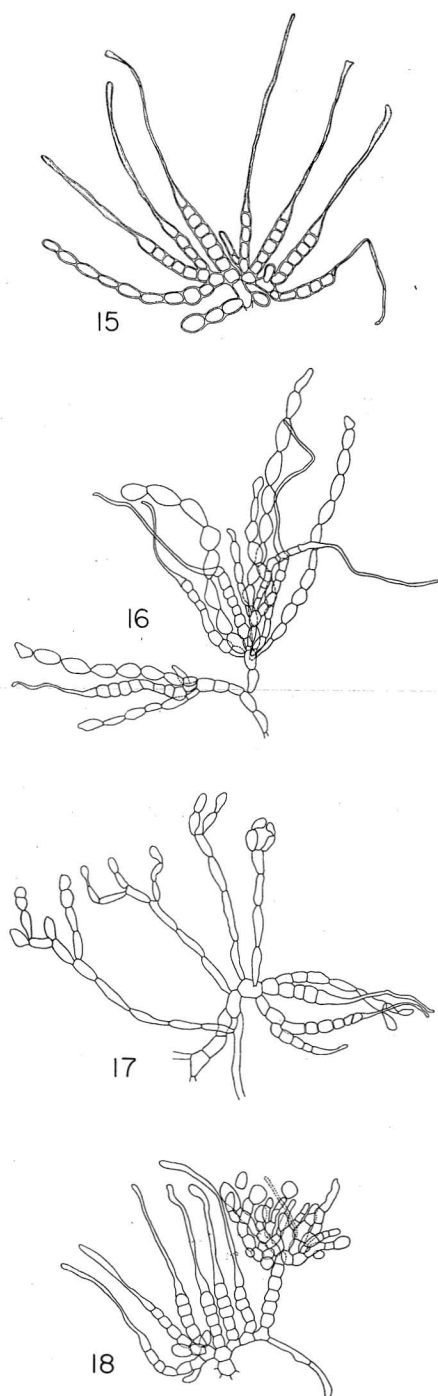
schrammi, where he found the carpogonial branches to be both terminal and otherwise. Our study leads us to believe that the vegetative morphological differences and the carpogonial branch differences between these two species may be due to age.

The Philippine collection may be divided into thalli of two sorts on the same basis used by Boergesen (1915) for distinguishing *Nemalion schrammi* and *N. longicolle*. The coarser of the two (as in *N. schrammi*) was whiter (more calcified) when alive; now dry, it is more yellow or brown in color, the axes are usually about 1.5 cm, but up to 3.3 cm, broad on the herbarium sheets. The surface is more strongly reticulate (i.e., the reticula are morphologically distinguishable). The more delicate form of the two was pinker (less calcified) when alive; now dry, it is still the pinker in color, the axes are only rarely over 1.0 cm broad; and the surface is more aereolate than reticulate (i.e., the reticulum is distinguished predominately by color).

Boergesen (1915) does not mention calcification and, indeed, basing his studies on exsiccata of previously wet-preserved materials, classified his two species as members of *Nemalion*, a genus generally considered to be noncalcareous. Neither Maze and Schramm nor Agardh mention liminess. After decalcification our own quite limy specimens strongly resembled the specimens of Boergesen's taxotype.⁷ Boergesen's specimens produced some gas when we put strong hydrochloric acid on them.

⁷ The term "taxotype" is employed by the present authors to designate a specimen used by an individual as either typical of a taxon or as the element in the taxon to which other elements are compared. It is, thus, a standard for taxonomic purposes, rather than a nomenclatural standard for application of priority by means of the type method.

FIGS. 5-14. Reproductive structures of *Liagoropsis schrammi*, drawn with the aid of a camera lucida from the various collections studied. The sizes are indicated by the index lines provided for the different figures. In general no attempt was made to indicate pit connections or the thickness of the gel or wall material surrounding the cytoplasts. Fig. 5, Spermatangial clusters, with a dotted line to indicate the outer limit of the gelatinous walls around the individual spermatangia. In spreading the spermatangia sufficiently to show some of their relationship to the stalks bearing them, several were broken away from the cluster and lost. (Type specimen of *Liagoropsis maxima* Yamada.) Figs. 6, 7, Monocarpogonial cortical branch systems bearing carpogonial branches, as well as spermatangial clusters. A rhizoid (rh) is shown at the base of the cortical system near the medullary (med) strands. Respectively, M. Doty nos. 19687 and 16954. Figs. 8-14, Gonimoblast development as generally found in all collections. Respectively, M. Doty no. 16954; cotype of *Liagoropsis maxima*; M. Doty no. 16954; M. Doty no. 16954; type of *Nemalion schrammi*; cotype of *Liagoropsis maxima*, and type of *Nemalion longicolle* [Boergesen no. 1614b].



100μ
FIGS. 15-18

Morphology of the male structures (Fig. 5) has proven of little value to us in the taxonomy of this genus, nor has the fact that some collections are monoecious and some dioecious been of value. Our Philippine material (no. 16954) is monoecious, as Desikachary (1957) reports to be the case in his material, whereas Yamada reports (1944:21) dioecious material. We have substantiated this latter point by our study of Yamada's specimens. Boergesen apparently did not see convincing evidence of spermatium production in either of the specific taxa he recognized, but expected his material of at least one of them to be dioecious.

SYSTEMATIC DISCUSSION

Though often in *Liagoropsis* they are solitary (Figs. 7, 8), usually one finds many carpogonial branches in clusters (Figs. 15-18). Figure 156C in Newton's book (1931) illustrates a similar situation for *Nemalion*, and see Boergesen (1915: fig. 68) for the same situation in *Liagora elongata* Zanardini, a species that perhaps should be transferred to *Liagoropsis*, along with some *Nemalion* spp. When the carpogonial branch clusters are large, containing five or more branches, their derivation seems clearly that of replacing vegetative (assimilatory) filaments. At one time we considered such "polycarpogonial" systems to be hair clusters with an occasional hair-bearing branch developing as a carpogonial branch. This was because at first we found many with short trichogynes and we interpreted them as hairs, for the hypogynous cells were not strongly differentiated. We now consider such to be merely young, for in almost each collection such branches in some clusters have been found bearing gonimoblast filaments. The similarities in hair and carpogonial development have been noted (e.g., Rosenvinge, 1911) by a good many authors. At least in ontogeny, in *Liagoropsis*, the determination process must remain labile for a long time and the hypogynous cells are never strongly specialized.

FIGS. 15-18. Polycarpogonial branch systems bearing, in one case, a gonimoblast. Respectively, type of *Nemalion longicolle* [Boergesen no. 1614b]; type of *Nemalion schrammi* from Paris specimen; M. Doty no. 16954; Boergesen no. 1614.

Perhaps the nature of the carpogonial branch itself is of systematic value. The straight carpogonial branch of *Liagoropsis* with a relatively large and somewhat variable number of not highly differentiated cells can be considered simpler than the curved carpogonial branches consisting of fewer, more highly differentiated and numerically and morphologically more uniform cells, for example, of *Helminthora*. In this respect *Liagoropsis*, *Nemalion*, *Trichogloea*, and *Trichogloeopsis* are similar.

Kylin (1956:108) distinguished *Liagoropsis* from *Nemalion* on the basis of the carpogonial branches, which in *Liagoropsis* were said to be accessory lateral⁸ branches on the cortical filaments, whereas in *Nemalion* the carpogonial branches were said to correspond to young branches of the cortical filaments. While this distinction may be useful for separating *Liagora*, *Helminthora*, and *Helminthocladia* from *Nemalion* or *Trichogloea*, it is not a valid one for distinguishing *Liagoropsis*, for this genus shows both derivations of the carpogonial branches but, particularly frequently, the more terminal, less specialized *Nemalion* type.

When the carpogonial clusters containing two or three carpogonial branches in a vegetative branch system are considered, the attachment and derivation of the different branches appear to be so different that some may be interpreted as replacing vegetative branches terminally (Figs. 12, 13), and others, either in the same (Fig. 15) or separate (Figs. 10, 11) fertile clusters, appear to have arisen laterally on, respectively, a carpogonial or a vegetative filament. In these small clusters the carpogonial branches also may seem to be attached to each other (Fig. 10), or in larger clusters they may appear to be (Figs. 15–18) parts of a cymose system. Thus the position or attachment of the carpogonial branches is not a very useful systematic criterion in this genus.

The first and subsequent divisions of the fertilized carpogonium do not show regularity and thus the sequences described by Papenfuss (1946) for various of the Helminthocladiaceae are not applicable to *Liagoropsis*. Some oblique

and some transverse divisions have been seen in the zygote contents as well as many cases where gonimoblast initials seem to have been produced without any division at all. No consistency was found. This is quite different from the situation in *Trichogloea* or *Helminthora*. This could be considered as primitive variability, whatever the unknown nuclear cytology.

The gonimoblast is small when compared to the size of the carpogonial branch. Its size is comparable to the cystocarp of *Nemalion* (Kylin, 1916), but in most other genera in the Helminthocladiaceae sensu Kylin the mature cystocarp is large and conspicuous and almost always associated with a large number of sterile filaments. The gonimoblast of *Liagoropsis* consists of but a few fertile filaments developing terminal carpospores on the more centrally formed filaments first. Subsequently carpospores are produced, also terminally, on the surrounding and later formed gonimoblast filaments. This sequence is not that of either *Liagora* or *Nemalion*. It would appear that the gonimoblast grows by producing young branches radially, which in age produce terminal carposporangia successively more distant from those first produced. This cymose development is not precisely the indeterminate growth of the gonimoblast initials described for the classical *Nemalion elminthoides* (Vell.) Batters (1902); nor is it that of *Trichogloeopsis*, where the primary gonimoblast filaments terminate in rhizoids. Neither does it, in its development, lead to the mixture of young, mature, and empty carposporangia characteristic of most *Liagora* species. In other words, it seems to be intermediate of, or perhaps more primitive than, these other two types.

In *Trichogloeopsis* (Abbott and Doty, 1960) and in *Nemalion*, as classically illustrated by Kylin (1956: figs. 57, 58A), the zygote divides transversely, and the primary gonimoblast filaments protrude radially and develop most at 90° or more from the trichogyne. With further growth the gonimoblast filaments curve toward the base of the carpogonial branch, and they may become parallel and close to it. The carpospores are produced terminally on secondary gonimoblast filaments which radiate or curve toward the outside of the thallus and which are branches of the primary gonimoblast filaments. Though differing in detail, the gonimoblast in

⁸ However, further on in his key and descriptions Kylin says "terminal or subterminal," but still places the genus near *Liagora* rather than near *Nemalion*.

Nemalion elminthoides collected at Pacific Grove, California, is similar to the above two genera in that a rather dense knotlike gonimoblast is produced wherein any filamentous nature is obscured.

In *Liagoropsis* (16954 and cotype of *L. maxima* Yamada) the gonimoblast filaments are loosely composed from the first and are clearly filamentous. This is another unique feature of *Liagoropsis* and was previously reported by Desikachary (1957) and is verified here by us. The gonimoblast filaments of *Liagoropsis* first appear (Figs. 8–11) straight and closely erect (i.e., they tend to parallel the trichogyne). These primary gonimoblast filaments differentiate (Figs. 12–14) carpospores at their tips later. The secondary gonimoblast filaments appear later as branches that are likewise erect and directed toward the exterior of the thallus. These secondary gonimoblast filaments arise from the nondifferentiated more basal cells of primary gonimoblast filaments and appear, when mature, as though they were sterile filaments surrounding and appressed to, or at least close to, the more matured primary filaments.

In the lack of sterile filaments, in the lack of a closely packed knot of gonimoblast initials, and in the direct growth of the gonimoblast initials toward the thallus surface, *Liagoropsis* is perhaps simpler than *Liagora* or *Helminthocladia*. In these two genera a knot of gonimoblast initials may form before the later formed filaments protrude toward the surface, and also sterile filaments may be present. At least sterile filaments of some kind are also present in *Trichogloea* and *Trichogloeopsis*. In this respect *Liagoropsis* is most like *Nemalion elminthoides*, which usually lacks the sterile filaments but has, apparently, the knot of cells developing from the zygote.

In surveying the genera of *Helminthocladia*-ceae, we have come to the conclusion that those with a low definite number of cells forming curved lateral carpogonial branches, with no vegetative cells between the hypogynous cells and the supporting cell, are more advanced than those which have larger and more variable numbers of cells forming straight carpogonial branches which often have one or more vegetative cells between the hypogynous cells and the supporting cell. In the first category with lateral

carpogonial branches which largely arise along the basal two-thirds of the supporting cell, are *Helminthocladia*, *Helminthora*, *Liagora* (*in sensu nostro*), *Dermonema*, and *Cumagloia*. In the second group, with terminal or lateral carpogonial branches, are *Liagoropsis*, *Nemalion*, *Trichogloea*, and *Trichogloeopsis*.

Desikachary (1962) interpreted the carpogonial branches of *Liagoropsis* as consisting entirely of hypogynous cells and the carpogonium. As noted above, it appeared to us that in some cases (e.g., Figs. 6, 11) there were cells of normal vegetative appearance at the base of the branch bearing the carpogonium, and in other cases (e.g., Figs. 7, 13, 18) none. We interpret this situation as evidence of primitive variability. Following our interpretation of the vegetative nature of some of these cells, we would say there were not even any "less well developed vegetative branches" arising from the carpogonial branches such as Desikachary (1957) shows in some of his illustrations.

The diffuse gonimoblasts of the two genera *Dermonema* and *Cumagloia* set them apart from all other members of this family.

Svedelius (1939), as a result of his study of *Dermonema*, thought Schmitz and Hauptfleisch's (1896) *Dermonemeae*, established for *Dermonema*, could well be treated as a separate family. Gardner (1917), as a result of his study of *Cumagloia*, thought they represented merely extremes in a family, the members of which had gonimoblasts of varying degrees of compactness. Desikachary (1962), in making a close study of the point, found *Dermonema* to be without the fusions, the earlier reported presence of which has led others to feel the genus might not belong to the *Helminthocladia*ceae at all. Desikachary, however, feels as we do, that there is not enough known about the related genera to justify establishment of a family for these two, and possibly other, genera at this time. Insofar as we know, no one has erected a familial taxon for this group. Should this be done it would appear, from the results of Desikachary's study, that this family should contain both *Dermonema* and *Cumagloia*.

In *Trichogloeopsis mucosissima* (Abbott and Doty, 1960) the carpogonial branches may occur in groups, somewhat similar to the clusters of carpogonial branches in *Liagoropsis* (Figs.

15–18); and it appears in both species that in this polycarpogonial condition the remaining nearby carpogonial branches are suppressed in their development after one of the group has begun to develop a gonimoblast. However, *Trichogloeopsis* differs from all Helminthocladiaceae in that it possesses sterile gonimoblastic rhizoids as daughter cells or continuations of the fertile system. In *Liagoropsis* there are no sterile cells associated with the gonimoblast, an unusual condition in this family.

The unique way in which the gonimoblast is formed from irregular division of the zygote (i.e., fertilized carpogonium) and the sequence of carpospore production would also lead us to believe that *Liagoropsis* is more primitive than any other member of this family—certainly more primitive than *Nemalion*, which has been used classically as a “primitive” red alga.

These latter two genera are rather distinctive in that the vegetative systems originating from the supporting cell tend to continue to grow beyond the carpogonial branches they produce, so that some of the carpogonia appear to be lateral in age but not by an epinastic development of the apex of the supporting cell. This lack of epinastic development of the supporting cell we consider to be one of the most primitive of the attributes of *Liagoropsis*.

Certainly, of the genera included in the Helminthocladiaceae by Kylin (1956), *Liagoropsis* is the least specialized and seems to stand with the simplest of the groups of genera we recognize. Table 2 presents our views of the general relationships of these major groups of genera and *Liagoropsis*. We (Abbott and Doty, 1960) have made a suggestion as to the family names, but have continued the use of Helminthocladiaceae above and in the title under which the present work was undertaken. We expect, however, to continue the use of the name Nemalionaceae for a family of algal genera of which *Nemalion* Duby (1830) is the type. We do not care to indicate a closer affinity for the Derronemeae at this time though, in relation to the lateral position of their carpogonial branches and the degree of specialization of their carpogonial branches, they would seem perhaps to be more closely related to the Helminthocladiaceae than to the Nemalionaceae. Similarly, and in agreement with Desikachary (1962), we do not

TABLE 2

FAMILIAL AND SUBFAMILIAL RELATIONSHIPS
AMONG THE MULTIAXIAL SIMPLER MARINE
GENERA OF THE NEMALIONALES USUALLY PLACED
IN THE HELMINTHOCADIACEAE BY
PREVIOUS AUTHORS

Nemalionaceae		Helminthocladiaceae
Nemalionaceae*	Derronemeae*	Helminthocladiaceae
<i>Liagoropsis</i>	<i>Cumagloia</i>	<i>Liagora</i>
<i>Nemalion</i>	<i>Derronema</i>	<i>Helminthocladia</i>
<i>Trichogloeopsis</i>		<i>Helminthocladiaceae</i>

* Schmitz and Hauptfleisch (1896) used Nemalionaceae and Derronemeae, respectively, for these two subfamilial groups. The former would have included our group Helminthocladiaceae as well.

feel it possible to postulate a generic phylogeny or family tree for the genera until more species have been studied in detail.

SUMMARY

One species, *Liagoropsis schrammi* (Maze and Schramm) Doty and Abbott, is recognized as occurring in both the western Atlantic and western Pacific, whereas three species have been recognized previously. The genus *Liagoropsis* is proposed for recognition as the simplest genus among the genera of a group we propose to treat as the Nemalionaceae, a subfamily suggested to include (in addition to the type, *Nemalion*) the genera *Liagoropsis*, *Trichogloeopsis*, and *Trichogloeopsis*. However, we recognize *Liagoropsis* to be quite distinct in several respects from these other three genera.

REFERENCES

- ABBOTT, I. A. 1945. The genus *Liagora* (Rhodophyceae) in Hawaii. B. P. Bishop Museum, Occ. Pap. 18(10):145–169.
— and M. S. DOTY. 1960. Studies in the Helminthocladiaceae. II. *Trichogloeopsis*. Amer. Jour. Bot. 47(8):632–640.
AGARDH, J. G. 1890. Florideae. In: Till Alg. Syst. Nya Bidrag, 6th Afd, p. 40.
BATTERS, E. A. 1902. A catalogue of the British marine algae. Jour. Bot. 40 (suppl.):1–107. (Not seen.)

- BERNATOWICZ, A. J. 1952. Seasonal changes in the marine algal flora of Bermuda. vi + 170 pp. (A dissertation on deposit in the University of Michigan library.)
- 1952. Seasonal aspects of the Bermuda algal flora. Papers, Michigan Acad. of Science, Arts and Letters 36:3-8.
- BOERGESEN, F. 1909. Some new or little known West Indian Florideae. Bot. Tids. 30: (reprint paged 1-19), pls. I, II.
- 1915. The marine algae of the Danish West Indies. Dansk Bot. Archiv 3(1):1-80.
- COLLINS, F. S., and A. B. HERVEY. 1917. The algae of Bermuda. Proc. Amer. Acad. Arts and Sciences 53(1):3-195.
- DESIKACHARY, T. V. 1957. On a "*Liagoropsis*" from Andamans. Revue Algologique II, 3:51-56, pl. 1.
- 1962. *Cumagloia* Setchell et Gardner and *Dermoneia* (Grev.) Harv. Jour. Indian Bot. Soc. 41(1):132-147.
- DOTY, M. S., and I. A. ABBOTT. 1961. Studies in the Helminthocladiaceae (Rhodophyta): *Helminthocladia*. Pacif. Sci. 15:56-63.
- DUBY, J. E. 1830. Botanicon gallicum, ed. 2, part 2, p. 959. (Not seen.)
- GARDNER, N. L. 1917. New Pacific Coast marine algae I. Univ. Calif. Publs. in Botany 6(14):377-416.
- HOWE, M. A. 1918. Algae, pp. 489-540. In: N. L. Britton, Flora of Bermuda. XI + 585 pp.
- 1920. Algae, pp. 553-631. In: N. L. Britton and Millspaugh, The Bahama Flora. VIII + 695 pp. Privately published by the authors, New York.
- HUERTA, L. 1960. Lista preliminar de las algas marinas del litoral del estado de Veracruz. Boletín Sociedad Botánica de México 25:39-45.
- KYLIN, H. 1916. Ueber die Befruchtung und Reduktionsteilung bei *Nemalion multifidum*. Ber. deutsch. bot. Ges. 34:257-271.
- 1956. Die Gattungen der Rhodophyceen. xv + 673 pp. C. W. K. Gleerups Press, Lund, Sweden.
- MAZE, H., and A. SCHRAMM. 1870-1877. Essai de classification des algues de la Guadeloupe, ed. 2. xix + 283 + iii pp. Basse-Terre, Guadeloupe. (See Wm. R. Taylor, Contr. U. S. Nat. Herb. 28:550 f., 3d ed.)
- NEWTON, LILY. 1931. A handbook of the British seaweeds. xiii + 478 pp. British Museum (Natural History), London.
- PAPENFUSS, G. F. 1946. Structure and reproduction of *Trichogloea requienii*, with a comparison of the genera of the Helminthocladiaceae. Bull. Torrey Bot. Club 73(5):419-437.
- ROSENVINGE, L. KOLDERUP. 1911. Remarks on the hyaline unicellular hairs of the Florideae, pp. 203-215. In: Biologiske Arbejder tilegnede Eug. Warming . . . (4) + 298 pp. H. Hagerups Forlag, Copenhagen.
- SCHMITZ, FR., and P. HAUPTFLEISCH. 1896. Helminthocladiaceae. In: A. Engler & K. Prantl, Die natürlichen Pflanzenfamilien . . . I(2):327-335.
- SVEDELIUS, NILS. 1917. Ueber die Homologie zwischen den männlichen und weiblichen Fortpflanzungsorganen der Florideen. Ber. deutsch. bot. Ges. 35(3):225-233.
- 1939. Anatomisch-entwicklungsgeschichtliche Studien ueber die Florideengattung *Dermoneia* (Grev.) Harv. Botaniska Notiser 1939:21-39.
- TAYLOR, W. R. 1942. Caribbean marine algae of the Allan Hancock Expedition, 1939. Allan Hancock Atlantic Exped., rept. no. 2, 193 pp. Univ. S. California Press, Los Angeles, Calif.
- 1951. Structure and taxonomic status of *Trichogloea herveyi*. Hydrobiologia 3(2):113-121.
- WILLIAMS, L. G., and H. L. BLOMQUIST. 1947. A collection of marine algae from Brazil. Bull. Torrey Bot. Club 74(5):383-397.
- YAMADA, Y. 1938. The species of *Liagora* from Japan. Sci. Papers of the Inst. of Algological Res., Faculty of Sci., Hokkaido Univ. 2:1-34, 22 text figs., 15 pls.
- 1944. Notes on some Japanese algae, X. Sci. Papers of the Inst. of Algological Res., Faculty of Sci., Hokkaido Univ. 3:11-25.